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CEPHALIC HOMOLOGIES. A CONTRIBUTION TO THE DETERMINATION OF THE ANCESTRY OF VERTEBRATES.[1]

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1. THE AFFINITIES OF AMPHIOXUS.

That Amphioxus has affinities both with Tunicates and with Vertebrates is, with our present knowledge, quite clear; but the relative degree of affinity on the two sides has not been settled. Amphioxus was originally classed with the fishes, but is now universally separated from them. Perhaps the most usual opinion is, that which classes Amphioxus with the Vertebrata, and divides the Vertebrata into two groups:—

I. CEPHALOCHORDA, (*Amphioxus*).

II. VERTEBRATA PROPER, (*Craniota*).

This division recognizes the fact that Amphioxus differs fundamentally from all the true vertebrates, but holds that the concept "Vertebrata" must be greatly extended and essentially modified, so as to admit the lancelet. The first writer known to me to deny that the Branchiostoma could be classed as a vertebrate was Carl Semper in 1875. This position has hitherto found little favor. Nevertheless, I hold that Amphioxus is more closely related to the Tunicates than to the Vertebrates, and that we ought to establish a group, which might be named Atriozoa, and would comprise Amphioxus and Tunicata.

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[1] Read before the British Association for the Advancement of Science, at Toronto, Canada, August 20, 1897.

The systematic value of embryology has been hitherto little recognized, but it certainly is of the greatest significance. It is not true that embryos are alike; on the contrary they show class, ordinal and generic differences from one another. I think, therefore, great stress must be laid upon the very close similarity in the embryonic development of Amphioxus and Tunicates. The fact of this similarity is now so familiar that it is superfluous to dwell upon it. On the other hand, it is desirable to renew attention to the large factor, which interpretation becomes, as soon as we attempt to establish a similarity between the ontogeny of Amphioxus and of the Vertebrates.

As regards the adult organization. The entire absence of lateral eyes and of lateral ears sharply separates both Tunicates and Amphioxus from the Vertebrata, while in the sense organs, they do possess, namely, the pigment spot or so-called eye, and the so-called olfactory pit, they are closely similar to one another, and quite unlike vertebrates. The attempt to identify the eye of Amphioxus with the pineal eye rests upon sheer speculation, and assumes that an organ developed in front of the neuropore is identical with one developed behind it. As regards the "olfactory pit," Kupffer's attempt to demonstrate a lobus olfactorius impar in Vertebrates is obviously unsuccessful. The atrium is another feature common to the Atriozoa, and is so highly distinctive, that it affords, what seems to me, an appropriate name for the whole group. The differences in the development of the atrium in the two classes of the Atriozoa are not, it is generally believed, such as to upset the homology, which is commonly maintained. The pharynx with its endostyle and ciliated bands, shows almost identity in Tunicates and Amphioxus, but only remoter resemblance to the Vertebrate pharynx, even to that of Ammocoetes with its hypobranchial groove. The gill clefts of

Amphioxus, both by their large number and by their peculiar subdivision, by secondary bars, resemble strikingly Tunicate gill clefts, but differ strikingly from those in any of the true vertebrates. How far the sexual organs of the cephalochorda and urochorda are comparable is not yet clear, but they show this striking resemblance that, in both, the sexual elements are discharged by dehiscence and pass through the ectoderm into the atrium, whereas in all vertebrates the sexual elements are discharged into the body cavity, or a duct derived from the body cavity. The excretory organs of Amphioxus in their association with the gills, and in their exterior or ectodermal openings show features which cannot be considered vertebrate, but I venture to express the expectation that homologous organs will be found in Tunicates. Finally as regards the central nervous system, the resemblance, which is almost identity, between Tunicates and Amphioxus has been often emphasized, but if we follow Howard Ayers in his attempt to homologize the parts of the brain in Amphioxus with those in true Vertebrates, we shall become only more and more impressed with the wide divergence between the two.

There remains the muscular system, which presents a striking and genuine resemblance to the metameric musculature of fishes, despite the secondarily acquired asymmetry in Amphioxus. It is a singular coincidence that some of those, who consider the segmentation of the body morphologically so insignificant, that it has no value to prove the kinships of Annelids and Amphioxus, yet consider it of great importance as evidence of the relationship of Amphioxus to the Vertebrates. But if we consider Amphioxus as a type intermediate between Annelids and Tunicates, the segmented musculature has been lost in the latter, an hypothesis which seems to me plausible, for as I have pointed out in my essay on "Senescence and Rejuvenation," all evolution of animals depends not only on the acquisition of characteristics, but also very largely on the loss of characteristics; this loss, as exemplified in the gill clefts and arches of the higher Vertebrates, affects the early embryonic stages, apparently to allow the embryonic material to undergo a new development. The assumption that the Tunicates have lost segments offers fewer difficulties than the assumption that they acquired segments to develop into the vertebrate type.

If morphological evidence has any value whatever, the conclusion seems to me inevitable that the Tunicates and Amphioxus constitute a natural group, Atriozoa, which are somewhat distantly allied to the Vertebrata.

2. THE CHORDATA.

Zoologists are generally agreed that the Chordata is a natural group, in the sense that the Tunicates, Amphioxus and Vertebrates are more closely allied to one another than with any other known animals. I can find no reason for dissent from this view, it therefore suffices to follow those who have insisted that the problem of the origin of Vertebrates is part of the problem of the origin of Tunicates.

3. THE PRINCIPAL THEORIES OF THE ORIGIN OF VERTEBRATES.

It is, in my judgment, unnecessary to discuss the theories of Adam Sedgwick as to the origin of metameric segmentation,[2] or of Hubrecht that the Nemertines are the ancestral type from which Vertebrates have sprung. The latter I have discussed previously. Of the former I will only remark in passing that it seems strange that Sedgwick has persistently denied the concrescence theory of the embryo, and yet puts it forward as a new idea upon which he founds his hypothesis of metamerism.

There are five theories known to me which certainly require consideration, namely, Gaskell's, Patten's, Bateson's, and the Appendicularia and Annelid theories.

A. *Gaskell's theory* was ably presented in Dr. Gaskell's address, delivered last year at Liverpool before the Sections of Physiology and Zoology. The main points in this theory are that the Vertebrata arose from Crustacea like animals, the intestine of the latter becoming the tubular nervous system of the former, while a pharynx arose by the concresence of branchiate crustacean legs, the spaces between the legs becoming gill clefts. There are two fatal objections to this theory. I consider it a first and sufficient objection that it sets aside the evidence that the primary germ layers, ectoderm and entoderm are homologous throughout the metazoa. The evidence on this point is overwhelming. Gaskell's theory leaves a heart between the pharynx and the nervous system, so that to save his theory he has to make two supplementary hypotheses, first, that the crustacean heart disappears, and second, that a new or vertebrate heart is formed by the tips of the legs where they grow together. It is, indeed, difficult to give morphological credence to these two hypotheses. If Gaskell's hypotheses were true, we should expect to see some trace in the ontogeny of Vertebrates of the development of the pharynx by the concrescence of solid outgrowths, but, as well known, the pharynx is a series of hollow entodermal evaginations. As regards the neuron, Gaskell supposes that the ependyma represents the epithelium of the crustacean intestine, while the nervous matter represents that which collects in the walls of the crustacean intestine. This view, which is essential to his hypothesis, overlooks the fact that in Vertebrates the same epithelium produces both ependyma and nerve cells. Very numerous other objections can be raised, and consequently I am ready to go so far as to maintain that the acceptance of Gaskell's theory is impossible.

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[2] Of course, not because the theory does not need consideration, but because it deals not directly with the origin of Vertebrates, but with the origin of segmented animals.

B. *Patten's theory* seeks in the Arachnid type the ancestral form of Vertebrates. Under Arachnids Patten includes the Arachnida *sensu strictu*, and the Trilobites and Limulus also. It is noteworthy that the original articles by Patten and Gaskell appeared in the same number of the *Quarterly Journal of Microscopical Science*, (August, 1890). I have often wondered whether the juxtaposition was due to editorial design. Patten rests his case chiefly upon comparison of the nervous system, and makes only somewhat uncertain and tentative suggestions, as to the three serious difficulties offered by vertebrate characteristics, namely, 1, the disappearance of the invertebrate and origin of the vertebrate mouth; 2, the origin of the pharynx; 3, the origin of the notochord. Under these circumstances it is inevitable that the whole hypothesis seems highly tentative. Patten emphasizes the fact that the brain and oesophageal commissures of Arachnids form an angle with the ventral nerve chain, and he compares this with the head bend of Vertebrates, and seeks to homologize the supraoesophageal and suboesophageal nerves with these of Vertebrates. After a careful study it seems to me that he fails to render these comparisons morphologically justifiable. This failure does away with the only important argument offered by Patten.

C. *Bateson's theory* that Balanoglossus represents an ancestral type of the Chordata has attracted considerable attention, and Wiley apparently considers the theory proven. Bateson seeks to demonstrate a close homology between Balanoglossus and Amphioxus. Yet according to his own observations the structure of Balanoglossus is extremely different in every organ and in every part of every organ from what is found in Amphioxus, except as regards the pharynx, where there occur striking resemblances in the disposition of the gill bars. But Spengel has demonstrated that these are resemblances only, and that the arrangement of the bars in Balanoglossus is so fundamentally different from that in Amphioxus that it is out of the question to deduce one from the other. Again, according to Bateson's observations on the development of Balanoglossus, Tornaria is one of the forms least like the embryonic lancelet, for it entirely lacks the segmented mesoderm, the notochord and elongated medullary plate. Bateson, in my opinion, has drawn exactly the reverse of the conclusions as to the phylogenetic value of Balanoglossus, which are warranted by his own published observations. Spengel's criticisms of Bateson's theory are so conclusive, that it is superfluous to go over the ground again. But two points may be briefly mentioned, if only to escape the charge of trifling with the theory. Bateson lays much emphasis upon a structure, which he names the notochord of Balanoglossus; this so-called "notochord" is a short diverticulum of the cephalad end of the alimentary canal, running into the proboscis; this diverticulum remains hollow throughout life; whether it is of entodermal origin or not is unknown; Spengel considers it probably ectodermal. A notochord is a band of entodermal cells differentiated along the dorsal median line and ending originally at the blastopore, with the walls of which it is fused, and it lengthens by additions at its blastoporic end; it is never hollow and never a canal. These characteristics of a notochord are invariable, but not a single one of them pertains to the alleged notochord of Balanoglossus. The question arises, if two organs are found to have no resemblance to one another, is their homology demonstrated? Surely, a morphologist can give but one answer. My second point touches upon Bateson's views concerning metamerism. These views are based on the tacit assumption that serial repetition of organs or parts, even if irregular, is the same as segmentation of the body. But embryology had demonstrated, before Bateson's time, the true morphological basis of metamerism in segmented animals. This basis is the division of the mesothelium, as above stated, into paired symmetrical blocks. That this is the case is not an opinion, it is merely the summary statement of thousands upon thousands of direct observations. Serial repetitions, therefore, of ectodermal or entodermal organs, without these mesothelial segments, are morphologically not segmentation. Bateson's assumption that there is, what we may name a "*miscellaneous metamerism,*" which, beginning in various parts, may lead on to true mesothelial metamerism is contrary to all morphological canons. That he considers this assumption necessary is another indication of the inherent weakness of his case.

So far as knowledge and discussion have brought us to-day, morphology has the choice between the two theories as to the origin of Vertebrates, the Appendicularia and the Annelid theory. A decision between these two alternatives, which shall be convincing to zoologists, is not at present possible, yet something, I think, may be determined as to the probabilities of the final choice.

D. The *Appendicularia theory* is the direct outcome of Kowalewski's embryological researches, and has been the subject of general attention from zoologists for a quarter of a century past. The full and able defense of it by W. K. Brooks in his Salpa monograph is so recent and well-known that it will suffice to recall that the theory assumes that Appendicularia is near the ancestral pelagic type of the Chordata; that it gave rise to a form with multiple gill openings leading to Tunicates, and by the further acquisition of segmental structure leading to Amphioxus, and from this last on to the true Vertebrata. It must be carefully noted that by the Appendicularia theory the prime morphological importance and significance is attributed to the notochord and the branchial pharynx, and a secondary importance to the metamerism, while the Annelid theory reverses this and attributes prime importance to the metamerism, and secondary to the notochard and pharynx.

E. The *Annelid theory* was founded independently by Dohrn and Semper, and has always been supported in my opinion by far more numerous and sounder arguments than any other theory of Vertebrate descent, with possibly the exception of the Appendicularia theory. The fullest presentation known to me, of the Annelid theory, is that by Hugo Eisig in his monograph of the Capitellidæ. Those, who have had theories of their own to defend, have never attempted (ought we not say, have never dared tc attempt?) to confute the Annelid theory. Sedgwick, Bateson, Willey, Gaskell, Patten, Morgan and others have either left the subject alone, or at most, have spoken slurringly and in disparagement of it, so that there are literally no important direct criticisms against the theory known to me. I take this to signify that the writers in questiod have attacked the problem of the ancestry of Vertebrates not in a judicial but in a somewhat partisan spirit.

4. APPENDICULARIÆ VS. ANNELIDA AS THE ANCESTORS OF THE CHORDATA.

The most essential difference between the two theories under consideration is formulated above in the paragraph on the Appendicularia theory. The alternative of choice between the two theories hinges upon the interpretation of Amphioxus which we accept, i. e.:

1. Is Amphioxus a Tunicate becoming a Vertebrate by the acquisition of segments?

2. Is Amphioxus an Annelid becoming a Tunicate by the acquisition of a notochord and gill bearing pharynx?

Of course, we all understand that Amphioxus is probably not the exact transitional form, but merely the nearest living ally, known to us, of the transitional form.

5. FURTHER AFFINITIES OF AMPHIOXUS.

We have already maintained that the nearest affinities of Amphioxus are with the Tunicates. We now are confronted by the question: Are its affinities on the other side closer with A, the Vertebrates, or B, the Annelids? Here I believe we we must start with the decision to leave the pharynx and notochord out of consideration, because these structures are characteristic of the Chordata as a whole and not of the Vertebrata. But there are three sets of organs in Amphioxus which offer special peculiarities morphologically; these are the segments, the sexual organs and the excretory organs. Let us consider these in order.

1. *Segments.*—The mesothelial segments of Amphioxus arise with their cavities in open communication with the archenteron. Ray Lankester has advanced, and O. Hertwig and others have adopted, the hypothesis that the coelom of Vertebrates is an enterocoele, but hitherto, although special investigations have been made, no conclusive evidence has been found that in any true Vertebrate there is a clear resemblance in the early condition of the mesoderm to the disposition characteristic of Amphioxus. Traces of evagination of the mesoderm along the edge of the notochord, as required by the enterocoele theory, have been described in various Vertebrate embryos by a number of authors. These traces are so slight and so variable, that I believe they would be considered as meaningless variations in the grouping of cells, similar to those occurring in other parts of the same embryos, were investigators not unduly influenced by the preconceived theory. No investigator has claimed, so far as I am aware, that any Vertebrate exhibits segmentally arranged mesoder-

mic diverticula. In other words, even if Lankester's enterocoele hypothesis holds true of the Vertebrates, they would still show only a very remote resemblance with Amphioxus so far as the early stages of the mesoderm are concerned. But there is yet another important difference between Amphioxus and the Vertebrates, namely, in the former the segments are total, in the latter partial. In Amphioxus the whole of the mesothelium is segmented, in Vertebrates only the dorsal regions of the mesothelium are segmented, the ventral regions or walls of the splanchnocoele are not segmented. That there is an impressive similarity between the formation of the mesodermic bands in Amphioxus and Annelids was shown by the discoveries of Hatschek, and in both types the segments are total. It is perfectly clear, therefore, that the early history of the mesoderm indicates a much closer affinity of Amphioxus with the Annelids than with the Vertebrates. The existing differences may be explained by the assumption that the cavities of the segments are formed in Annelids after, in Amphioxus during, the morphological separation of the mesoderm from the entoderm.

2. *Sexual organs.*—The sexual organs of Amphioxus are confined to the branchial region, they are segmentally arranged and they are lateral of the excretory organs. Those of Vertebrates do not appear in the branchial region, they are not segmented and are mediad of the excretory organs. The view that the sexual organs are developed from segmental anlages has been advanced, and such anlages have been named gonotomes. I have shown elsewhere, that this view is based upon an incomplete consideration of the facts, and recently C. Rabl has fully confirmed my arguments. In Annelids the sexual organs are segmented, and are so disposed that we can understand how, from an Annelid ancestor, they may have given rise to the disposition found in Amphioxus, but, unfortunately, no careful study of such possible comparisons is known to me. Evidently a direct comparison of the sexual organs of Amphioxus with those of Vertebrates involve the most serious difficulties, while the comparison with Annelids promises well.

3. *Excretory organs.*—Boveri has shown that the excretory organs of Amphioxus are tubules which begin with a ciliated internal funnel and open through the ectoderm, and that their primitive arrangement is probably segmental; they are confined to the branchiate region. They differ, therefore, from the segmental organs of Vertebrates, which open into a longitudinal internal duct, and occur only behind the branchiate region. It is true that the attempt has been made to show that the duct is originally derived from the ectoderm, but the weight of evidence—see especially Price on Bdellostoma, and Rabl on Elasmobranchs—is at present against this view and in favor of the mesothelial origin of the duct. In Annelids segmental organs have the same arrangement as in Amphioxus, they open directly through the ectoderm, and they also may occur in that part of the body which, on the theory of Annelid ancestry, must have been evolved into the pharynx. The morphology of the excretory organs is thus readily perceived to indicate the Annelidian rather than the Vertebrate relationships of Amphioxus.

And now I ask, must we not conclude that Amphioxus is a Chordate nearly related to Tunicates, more remotely related to Vertebrates, and revealing in its organization important differences from other Chordata, which differences demonstrate a true kinship with Annelids? Now certainly no one would venture to regard Amphioxus as the ancestor of the Annelida, hence we are obliged to consider the Annelida as representing the ancestral type of the Cephalochorda, and, therefore, of all Chordata.

b. *The position of Appendicularia.*—The conclusion just stated involves the assumption, so far as now appears, that Appendicularia is not an ancestral but a secondary type. But Appendicularia much resembles a young stage of other Tunicates (free swimming larvæ), and we have learned to trust so much to the law of recapitulation (Haeckel's Biogenetisches Grundgesetz) that it is hard to believe that it does not govern Appendicularia, which would then be of the phylogenetic significance assumed by W. K. Brooks, whose argumentation is so strong, that even while defending the Dohrn-Semper theory, one must have in reserve readiness to change sides.

7. ORIGIN OF VERTEBRATA.

If the Annelids gave rise to the Chordata, we must consider the possible origin of certain anatomical characteristics of the Vertebrates, *sensu strictu*. Of such characteristics three are specially prominent, the general arrangement of the mesoderm, the pronephric duct, and the head with its arrangement of mouth, brain and eyes so unlike that in Annelids.

1. *The mesoderm* of Vertebrates, as already remarked, is characterized by having a large splanchnocoele and by being segmented only in its dorsal or epiaxial part. In Amphioxus the mesoderm is at first totally segmented as in Annelids, and later develops a splanchnocoele, and assumes in other respects an arrangement (of sclerotome and cutis plate) wonderfully comparable, according to Hatschek, with the vertebrate type of mesoderm. Amphioxus seems to really afford the key for the transition of the mesoderm from the Annelid to the Vertebrate type, and the occurrence of the actual transition ontogenetically renders it natural to advance the theory of the corresponding transition phylogenetically, thus obviating one of the former difficulties in the Annelidan theory of the origin of Vertebrates.

2. *The pronephric duct*, (often referred to as the Wolffian duct). This is a longitudinal epithelial tube, into which the segmental organs of Vertebrates open. Hatschek, in his paper on Polygordius, suggested that the segmental organs might acquire a direct secondary connection with one another; a series of such connections would make a longitudinal duct. Edward Meyer found such connections in adult Annelids, and other instances are known, see Willey's Amphioxus, 80–82. Price's observations on the Californian Myxinoid, and Rabl's on Elasmobranchs, tend to show that this is the actual origin of the duct. We no longer, therefore, need to take refuge in Haddon's or Boveri's hypothesis of the origin of the duct, since Hatschek's theory is sufficient and is supported by such actual evidence as we possess.

3. *Cephalic homologies.*—Up to this point we have dealt with knowledge and ideas derived from previous scientific publica-

tions, and have done little more than attempt to present the problem critically. As regards the head, however, even theories have hitherto failed us, and no hypothesis as to the evolution of the vertebrate head from the Annelidan type has been brought forward, which could not be shown to encounter insuperable objections, or at least which appeared insuperable to those who were opposed to the Annelidan theory. The suggestion most widely known and discussed is that the invertebrate mouth disappeared, the oesophageal ring with the neighboring ganglia formed the vertebrate brain, and a new vertebrate mouth was evolved, according to Dohrn, by the fusion of two gill clefts in the ventral median line.

I ask your consideration for an entirely different theory of the homologies of the vertebrate head. A morphologist must feel grave hesitation in assuming that such important structures as the main lateral eyes and as the oral evagination should have totally disappeared during the evolution of Vertebrates, for they are an advancing type, not a degenerate type losing its organs. He must also feel grave hesitation in assuming that main lateral eyes have been evolved in the Articulates and Vertebrates without any genetic relationship. It is natural, therefore, to test the assumption that the articulate eyes and vertebrate eyes are phylogenetically homolgous, it being, of course, understood that the comparison excludes ocelli, accessory eyes in Annelids and the pineal eye of Vertebrates. We note at once that the visual sensory apparatus in both cases is epithelial in type, and is derived immediately from the ectoderm, and further that in both cases the sensory apparatus is directly connected with nervous substance, in Articulates the so-called optic ganglion, in Vertebrates the nervous tissue of the retina, and finally that in both cases there runs from the optic apparatus a fibre tract, which is not a nerve, but a commissure, that is to say, a differentiation of a part of the central nervous system itself; this tract we call a part of the oesophageal commissure of the Articulate, and the optic nerve of the Vertebrate. We are thus lead to the supposition that eyes and optic nerves represent in Vertebrates the main eyes, the supra-oesophageal ganglia, and the oseophageal commissures of the Articulates. Can this supposition be upheld? I do not think that the invagination of the optic vesicles in Vertebrates will be said by any morphologist to invalidate the comparison. At first it seems to reduce the so-called "brain" of Articulates to insignificance, but as we know that this brain, or more correctly, supra-oesophageal ganglion, is mainly a visual ganglion in Articulates, and it is by no means a great degradation for it to appear merely as a retina in Vertebrates. We must not be influenced by the misuse of the word "brain" applied to Invertebrates. But how can two diverging vertebrate eyes, which form a Y with the main nervous system, be the same as a complete nervous ring around the oesophagus? This difficulty is met by assuming that the eyes and optic ganglia fail to meet in the median line in front. In connection with this assumption, remarks upon two points are necessary. *First,* in Invertebrates with oesophageal nerve rings, the supra-oesophageal ganglia do not apparently arise in the median line, but as two symmetrical anlages, which subsequently meet in the median line. I recall that this is the method of development in Lumbricus (E. B. Wilson), Arachnids and Insects (Patten), Crustacea (Kingsley), and in Crepidula (Conklin). Other observations could be cited.[3] Hence we have only to believe that in the Vertebrates the separation is maintained and increased. *Second,* there should be found a cause for the separation of the eyes (supra-oesophageal ganglia) in the Vertebrates. This is given by the growth of the vertebrate brain, which is enormous and precocious. If the brain acquires great size, the eyes are correspondingly separated. It is evident that our assumption makes the brain homologous with the suboseophageal ganglia probably plus several ganglia of the ventral chain, the remainder of the ventral chain becoming homologous with the spinal cord.

Next as to the invertebrate mouth. If the eyes and optic nerves represent the oral nerve ring, we must look for the invertebrate mouth between the eyes. The invertebrate mouth is an ectodermal invagination, which has a direct or acquired open communication with the entodermal cavity or archenteron. Is there such an evagination in the Vertebrates? Unquestionably there is, and a large conspicuous and well known one, which gives rise to the olfactory pits and to the hypophysis proper. It is important to recall that the naso-hypophysal invagination is single, and we may homologize it with the Annelid ectodermal stomodaeum. It seems to me a very significant fact that in the lowest Vertebrates (the Myxinoids) the naso-hypophysal invagination opens through the entoderm into the pharynx. This connection, which has been known but the significance of which has remained obscure for three-quarters of a century, may, under the supposition we are considering, be interpreted as the survival of the Annelidan condition. In other Vertebrates (Petromyzon and Gnathostomes) the opening mentioned does not recur, although contact between the ectoderm of the invagination and the pharyngeal entoderm can, it is claimed, be observed in certain forms (Accipenser, etc). To avoid confusion, it must be pointed out that the hypophysis is only a part of the invagination, and neither it nor the general invagination are connected with the neuropore; the hypophysis of Vertebrates is, therefore, not homologous with the neuroporic pit, which Willey and others have erroneously named the hypophysis of Amphioxus and Tunicates.

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[3] That the observations are conflicting as to the paired origin of the Articulate brain is well known, but the theory that the median Scheitelplatte evolved into the Articulate brain encounters difficulties which seem to me very serious.

What is the actual vertebrate mouth? If we interpret the naso-hypophysal invagination as the homologue of the Annelidan mouth-gut, we find that the oral invagination is sepated from the hypophysal by a fold, which becomes the upper jaw in Cyclostomes, and which is present in the embryos of all Vertebrates. (In Anmiote embryos this fold forms a ridge between Seesel's pocket and the hyphophysis). It, therefore, still remains necessary to look upon the vertebrate mouth as a new acquisition. It seems to me that, under the new conception of the head, Dohrn's hypothesis is more promising than before. But beyond this I can add nothing to the explanations of the vertebrate mouth previously attempted.

The brain arose, by the present supposition, from the ganglia of the "ventral" chain of Annelids. Even in Articulata, in the Crustacea and Arachnida, we encounter a tendency of the thoracic ganglia to make a brain. If the brain did thus arise, its enlargement would cause, as we see in the Vertebrate embryo, the brain to expand forwards, and since there is no corresponding growth on the hæmal side, this expansion would cause the projecting head to bend over towards the hæmal (Annelid dorsal, or Vertebrate ventral) side, and thus carry the mouth into a new position, and at the same time prevent the eyes and praeoral ganglia from meeting in the median line and force the visual organs into lateral positions. We thus reach a natural and simple explanation of the difference between the Annelid and Vertebrate head. The conception brought forward is favored by the conditions observed in Myxine and Petromyzon, for the eyes in these forms are small, in Myxine without a lens. The large size of the eyes is a subsequent acquisition of the Gnathostomes. By my hypothesis we should expect the evolution of the brain to precede that of the eye in Vertebrates. Finally, the vertebrate brain, by our supposition, was segmented originally throughout, and that this idea is correct is indicated by the trend of recent opinions formed by investigators of the cephalic neuromeres, and the morphology of the cephalic nerves in the Vertebrata.

The series of considerations outlined justify the hypothesis presented, namely, the Vertebrate head was evolved from the Annelid head. The three principal factors in this evolution were: 1. The formation of the vertebrate brain from several of the post-oral ganglia of the ventral chain. 2. The preservation of the ectodermal mouth-gut (Vorderdarm) of Annelids as the naso-hypophysal invagination. 3. The conversion of the visual apparatus and supra-oesophageal ganglia, which are prevented from fusing in the median line by the enlargement of the vertebrate brain, into the vertebrate eyes (retina), the oesophageal commissures persisting as optic nerves.

If this hypothesis be ultimately verified and shown to be in full accordance with the facts, it will obviate those difficulties of the Dohrn-Semper Annelid theory of the origin of Vertebrates, which at present are the most serious.

One more point, the cephalic homologies advocated increase the morphological importance of the eyes, and further emphasize the divergence between Amphioxus and Vertebrates, and makes the absence of lateral eyes in Amphioxus more significant even than before, and affords a further justification for the union of Amphioxus with the Tunicata.

I have presented the subject in the merest outline, for almost every sentence might be expanded to a paragraph, often into a chapter, without making the treatment exhaustive, but I hope enough has been said to make the argumentation clear and to justify it.

The origin of Vertebrates is one of the most difficult and obscure problems which at present occupy the general attention of zoologists. I am well aware that my own studies have concentrated upon the embryology of Vertebrates, and that it is difficult, perhaps, impossible, for one man to have a first hand mastery through his own observations of all the evidence which must decide the final solution. I have expressed, therefore, not convictions, but probabilities, and must certainly reserve the right to adopt other conclusions than those above advocated. The rival theories have sometimes taken on a very positive tone, and their advocates have referred to the Dohrn-Semper theory as a thing of the past, discarded and quite disproved. This attitude is regrettable, and I hope, by showing that much can still be said in favor of the origin of Vertebrates from Annelids, to contribute towards a sober and judicial discussion of an important and interesting topic.

8. CONCLUSION.

It remains only to present the following simple and comprehensive phylogenetic table :—